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# Interspecific Tertiary Parasitoidism between Two Aphid Hyperparasitoids: *Dendrocerus carpenteri* and *Alloxysta megourae* (Hymenoptera: Megaspilidae and Cynipidae)

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*ABSTRACT*

The behavior of aphid hyperparasitoids is briefly reviewed, including their taxonomy and ecological impact. Interspecific tertiary parasitoidism between the ectophagous megaspilid *Dendrocerus carpenteri* and the endophagous cynipid *Alloxysta megourae* was studied. The primary parasitoid was *Aphidius smithi,* using the pea aphid, *Acyrthosiphon pisum,* as the host. During 17 test days available for attack by the second hyperparasitoid, *D. carpenteri,* on the host inside the dead aphid "mummy," its overall success was 31.4%. Tertiary parasitoidism, however, was not possible during all 17 test days. Although test days 1–8 resulted in average *D. carpenteri* emergence of 49.3%, tertiary parasitoidism was not in fact occurring during this period because the first hyperparasitoid, *A. megourae,* was still inside the *A. smithi* larva within the mummy. Only during test days 9–17, could tertiary parasitoidism be accomplished when the larva of *A. megourae* was feeding externally on its primary host larva, and was thus available to be attacked by *D. carpenteri.* Yet, even then, only on test days 9 and 10 did *D. carpenteri* reach a peak emergence of 50.0%. Thereafter, the success rate of tertiary parasitoidism declined markedly, so that the average emergence of *D. carpenteri* during the remaining test days 11–17 was only 8.1%. Host specificity by *D. carpenteri* may account for this decline.

## Introduction

Aphids are world-wide pests of agricultural crops, orchard and forest ecosystems. Fortunately, they are attacked by a number of natural enemies, especially by the two types of beneficial entomophagous insects: 1) *predators,* such as ladybird beetles (Coleoptera: Coccinellidae), and 2) *parasitoids,* such as the "parasitic" microwasps (Hymenoptera: Aphidiidae and Aphelinidae). These latter are the wasp parasitoids that serve as hosts for our present research. They are often called "parasites" in earlier

publications, but "parasitoid" is a more precise term which indicates that the host is killed by larval progeny, not by an adult female wasp that has oviposited into her aphid host.

## Primary Parasitoids

The beneficial wasp used in our experiments was the aphidiid parasitoid, *Aphidius smithi* Sharma and Subba Rao. It has only one host in which its progeny can develop: the pea aphid, *Acyrthosiphon pisum* (Harris). The female wasp has a typical oviposition behavior: after initial contact has been made with a host aphid by antennal tapping, she stands facing the aphid and bends her abdomen anteriorly beneath the thorax and between the legs. Then, by moving her abdomen forward, she quickly inserts her ovipositor into the aphid and deposits an egg in the hemocoel. The egg hatches, and there are four larval instars during which time the aphid is gradually devoured internally. After approximately 8 days, a fourth instar larva spins a cocoon inside the dead aphid, and the latter's skin becomes hard and turns from green to light brown, being referred to as a "mummy." The prepupal, pupal and preadult stages develop within the mummy over the next 4 days. Approximately 12 days after the egg was originally deposited inside the aphid, the new adult cuts a circular emergence hole in the dorsum of the mummy and pulls itself out. This hole has an attached lid made of mummy skin.

## Hyperparasitoids

As might be expected in such a plant-aphid-parasitoid complex, however, there is yet one higher trophic level, viz., that of the secondary parasitoids or hyperparasitoids. These Hymenoptera attack the beneficial primary parasitoids.[22, 24] Because of their interference with the impact of primaries on aphids, hyperparasitoids are considered detrimental to a biological control program, and are never purposely introduced into a region.[8, 10] There continues to be some debate, nonetheless, about the actual harm and even instead, the possible positive beneficial role of hyperparasitoids in maintaining a balance between populations of insect species in the ecosystem because multispecies complexity might help to effect community stability.[4, 9, 14, 16, 17, 18, 19, 21] Hence, aphid hyperparasitoids provide a microcosm for research on this fascinating and practical ecological puzzle.

## Taxonomy

Hyperparasitism and its associated behaviors evolved in three superfamilies of Hymenoptera: Chalcidoidea, Ceraphronoidea, and Cynipoidea.[8] A currently acceptable summary of the five families and nine genera of these aphid hyperparasitoids is given below:

1) **Superfamily Chalcidoidea:**
   a) Family Pteromalidae: *Asaphes, Pachyneuron, Coruna*
   b) Family Encyrtidae: *Aphidencyrtus*
   c) Family Eulophidae: *Tetrastichus*
2) **Superfamily Ceraphronoidea:**
   a) Family Megaspilidae: *Dendrocerus* (=*Lygocerus*)
3) **Superfamily Cynipoidea:**
   a) Family Cynipidae (Subfamily Alloxystinae): *Alloxysta* (=*Charips*), *Phaenoglyphis, Lytoxysta*

In order to examine possible relationships between taxonomy and behavior, it is useful to divide aphid hyperparasitoids into two major categories based on their larval feeding behavior: *endo*phagous and *ecto*phagous hyperparasitoids. In *endo*parasitoids, a female wasp deposits her egg inside a primary parasitoid larva while it is developing inside the live aphid before it is killed or "mummified," and then the hyperparasitic larva feeds internally on the primary larva. In *ecto*parasitoids, a female wasp deposits her egg on the surface of a primary parasitoid larva only after the aphid is killed and mummified, and then the hyper-

parasitic larva feeds externally on the primary larva, but still within the mummy. Therefore, in view of these two different behaviors of both the adult female wasp and her resulting hyperparasitoid larva, the taxonomic listing of genera given above can be rearranged to reflect their general behavior:

1) *Endo*parasitoids:
   *Alloxysta* (=*Charips*), *Phaenoglyphis, Lytoxysta,* and *Tetrastichus*;
2) *Ecto*parasitoids:
   *Dendrocerus* (=*Lygocerus*), *Asaphes, Pachyneuron,* and *Coruna*

*Aphidencyrtus aphidivorus* (Mayr) is a special case because it has a "dual" ovipositional behavior. Although it is in the category of being *endo*parasitic, it can attack the primary parasitoid larva either while the aphid is still alive as *A. megourae* does, or also after the mummy is formed in the manner of *D. carpenteri.* In both cases, however, the egg of the *A. aphidivorus* female is laid inside a primary parasitoid larva where it feeds as an endophagous hyperparasitoid. Hence, *A. aphidivorus* closely resembles the typical behavior of an endoparasitoid larva, yet the adult female can show both kinds of ovipositional behavior. Experiments have shown that when given a "choice" of hosts (primary larva either in a live aphid or in a mummy), the second of the dual attack behaviors is preferred, viz., oviposition into the primary parasitoid larva after mummy formation.[11]

## Tertiary Parasitoidism

Besides attacking primary parasitoids, aphid hyperparasitoids can also attack each other, resulting in *tertiary* parasitoidism. This has been demonstrated, at least in the laboratory, in several combinations of cases:

1) *Intra*specific tertiary parasitoidism or *auto*hyperparasitoidism:
   a) When a second adult aphid hyperparasitoid, *Dendrocerus carpenteri* (Curtis), successfully attacked and oviposited on a first *D. carpenteri* larva developing inside a dead aphid mummy. The progeny of the second *D. carpenteri* female fed as a larva on the first *D. carpenteri* larva and eventually emerged as an adult 16 days later.[1]
   b) When a second *Asaphes lucens* (Provancher) does the same to a first *A. lucens* larva, and emerges as an adult 21 days later.[13]
2) *Inter*specific tertiary parasitoidism or *allo*hyperparasitoidism:
   a) When the adult aphid hyperparasitoid, *Asaphes californicus* Girault, successfully attacked and oviposited on another aphid hyperparasitoid, *Alloxysta victrix* (Westwood). The larva of the *A. californicus* fed on the *A. victrix* larva inside the mummy and eventually emerged as an adult 21 days later.[20]
   b) When *Dendrocerus carpenteri* (Curtis) does the same by attacking the larva of *Alloxysta megourae* (Ashmead). This last example of interspecific tertiary parasitoidism forms the basis of this paper, and a brief introduction to the methodology of our research is given below.

In our study, the primary endoparasitoid, *Aphidius smithi*, was allowed to parasitize the pea aphid, *Acyrthosiphon pisum,* in the laboratory. The *A. smithi* egg hatched in 2 days and, under our laboratory conditions, after 6 days it would have developed into a fourth instar larva. However, on that day, the endophagous hyperparasitoid, *Alloxysta megourae* (Ashmead), was permitted to oviposit within the developing *A. smithi* larva that was slowly devouring the still live pea aphid (Table 1). The *A. megourae* egg hatches 2 days later, or about the same time as the *A. smithi* larva kills the aphid, spins a cocoon inside the dead aphid, and the "mummy" is formed. This would ordinarily occur on the eighth day after the *A. smithi* egg was initially deposited inside the live aphid.

After hatching, the *A. megourae* feeds in-

**Table 1.—Composite life cycles of a primary parasitoid, *Aphidius smithi,* and a first hyperparasitoid, *Alloxysta megourae,* in the pea aphid under experimental laboratory conditions when an aphid mummy is attacked by a second hyperparasitoid, *Dendrocerus carpenteri,* during the 17 test day period.**

| Age in days | *Aphidius smithi* | Age in days | *Alloxysta megourae* | 17 Test days | |
|---|---|---|---|---|---|
| 0 | Egg deposited in aphid | | | | |
| 1 | | | | | |
| 2 | 1st larval instar | | | | |
| 3 | | | | | |
| 4 | 2nd larval instar | | | | |
| 5 | 3rd larval instar | | | | |
| 6 | 4th larval instar | 0 | Egg deposited in *A. smithi* | | |
| 7 | | 1 | | | |
| 8 | Host aphid mummified[a] | 2 | Egg hatches | 1 | |
| | | 3 | | 2 | |
| | | 4 | 1st larval instar | 3 | |
| | | 5 | | 4 | |
| | | 6 | 2nd larval instar | 5 | |
| | | 7 | | 6 | *Dendrocerus carpenteri* has only 17 test days to attack the mummy[c] |
| | | 8 | 3rd larval instar | 7 | |
| | | 9 | | 8 | |
| | | 10 | Mature larva feeds externally | 9 | |
| | | 11 | | 10 | |
| | | 12 | Prepupa (meconium voided) | 11 | |
| | | 13 | Pupa | 12 | |
| | | 14 | | 13 | |
| | | 15 | | 14 | |
| | | 16 | Preadult | 15 | |
| | | 17 | | 16 | |
| | | 18 | | 17 | |
| | | 19 | Adult *A. megourae* emerges[b] | | |

[a] When hyperparasitized by *A. megourae,* the *A. smithi* larva ceases development.
[b] When hyperparasitized by *D. carpenteri,* the *A. megourae* will never emerge.
[c] If successful, an adult *D. carpenteri* emerges 16 days after its mother lays her egg.

ternally as an endoparasitoid on the *A. smithi* host causing the latter to cease further development inside the mummy. On the tenth day after the *A. megourae* egg was deposited, the larva emerges from the deteriorating *A. smithi* larva and feeds externally on its remains. The *A. megourae* completes its development while still inside the mummy, and becomes an adult on approximately the nineteenth day after oviposition. In emerging from the mummy, the adult cuts a distinctive jagged hole and will soon copulate if a mate is available.

The second hyperparasitoid is ectophagous, and so the *Dendrocerus carpenteri* (Curtis) female can attack her host only after the mummy is formed. In the sequence of events just described, the mummy is available for attack only during 17 days (Table 1). Our present research studied the results of permitting a *D. carpenteri* female to oviposit on the surface of whatever host was inside the mummy, i.e., either the *A. smithi* larva already parasitized by *A. megourae,* or the *A. megourae* larva itself. In both cases, an adult *D. carpenteri* would emerge approximately 16 days after its mother had oviposited. These experiments were conducted with replicates for each of the 17 available "test days."

## Materials and Methods

The pea aphid, *Acyrthosiphon pisum,* served as the laboratory host in this study, and was reared on broad bean, *Vicia faba* Linnaeus. The primary parasitoid was *Aphidius smithi,* and there were two hyperparasitoids: the endoparasitic cynipid *Alloxysta megourae*, and the ectoparasitic megaspilid *Dendrocerus carpenteri.* All insects were laboratory reared in a controlled

bioclimatic chamber according to the method described in an earlier publication.[1] The daytime (16 hr) temperature was 21.1 ± 0.6°C at 75 ± 5% RH, while nighttime (8 hr) temperature was 15.5 ± 0.6°C at 85 ± 5% RH.

Parasitizing the fourth instar aphid by the primary parasitoid wasp was done in a glass cylinder or "stinging-tube" used by Matejko and Sullivan.[15] This reference on the bionomics and behavior of *Alloxysta megourae* also detailed how an *A. megourae* female attacked and oviposited into a parasitized aphid containing a 6-day-old *A. smithi* larva. In our procedure, about 15–20 parasitized aphids were placed in the glass stinging-tube with 3–4 mated *A. megourae* females. After 6 hr, the hyperparasitoids were removed and the live, parasitized (and now hyperparasitized) aphids were returned to broad bean plants. Here, each hyperparasitized aphid remained on a plant while feeding normally until it was killed by a primary larva developing within it. The dead aphid became completely mummified within 24 hr. As shown in Table 1, this occurs about 8 days after the initial oviposition by an *A. smithi* female.

After 2 days, these mummies were removed from the broad bean plants and were placed in uncoated Dixie® containers covered with clear plastic covers. Only those mummies with "wound scars," indicating hyperparasitoidism by *A. megourae,* were used in the next step of the experiment on tertiary parasitoidism.[20]

Each aphid mummy parasitized by *A. smithi* and hyperparasitized by *A. megourae* is normally attached to the broad bean leaf. We did not pry the mummies loose from this substrate, but instead carefully cut out the broad bean leaf tissue around each mummy with a pair of fine scissors. This leaf area was needed by a female *D. carpenteri* because she uses it as a substrate on which to anchor herself as she backs into the mummy when she oviposits.[1] This oviposition behavior is unlike the two species in the genus *Asaphes* that had been studied earlier, viz., *A. californicus* and *A. lucens.* In these cases, the female climbs atop a mummy and oviposits through its dorsum.[12, 20] One such mummy was placed in a 60 × 15 mm, covered plastic petri dish into which one mated female *D. carpenteri* was introduced for 1 hr and then removed. Since a *D. carpenteri* female must first drill a hole through the mummy with her ovipositor, we used the presence of such a "drill hole" as proof that a particular mummy had at least been attacked. Mummies without such drill holes were discarded. The remaining experimental mummies were held for a minimum of 25 days to allow time for the two different species of hyperparasitoids (*A. megourae* or *D. carpenteri*) to emerge even if development were delayed. In our experiments, approximately 25 replicates were done for each of the 17 test days, making a total of 420 mummies that were used.

## Time of Attack

Our experiments on interspecific tertiary parasitoidism were based on the time sequence of development inside the mummy of the first hyperparasitoid as summarized above in the introduction and in Table 1. Because *D. carpenteri* attacks its host only after formation of a mummy by an *A. smithi* larva, our experiments on interspecific tertiary parasitoidism were limited to 17 "test days," i.e., from mummy formation (which coincides with hatching of an *A. megourae* egg) to the day before emergence of *A. megourae* as an adult from the mummy.

## Results and Discussion

### *Success Rate of Tertiary Parasitoidism*

Of the 420 mummies that had definitely contained both hyperparasitoids, 341 adult hyperparasitoids emerged. Non-emergence or mortality of the remaining 79 mummies will be discussed later. During the 17 test days available for attack by the second hyperparasitoid, *D. carpenteri,* its mean success rate was 31.4%. However, as in the three earlier reports on similar experiments

involving two hyperparasitoids, *Asaphes californicus* and *Alloxysta victrix,*[20] *Dendrocerus carpenteri* and *D. carpenteri,*[1] or *Asaphes lucens* and *A. lucens,*[13] a first hyperparasitoid is not always directly available for attack as a host. In our experiments, the vulnerability of *A. megourae* depends on its developmental stage and the time sequence of the 17 test days. Hence, regardless of which hyperparasitoid (first or second) eventually emerges as an adult, true tertiary parasitoidism may not have occurred. In this case, the endophagous *A. megourae* larva feeds within an *A. smithi* primary larva during the first 8 test days. *A. megourae* could not be attacked directly, therefore, because the ectophagous *D. carpenteri* larva is feeding on the surface of whatever host is inside a mummy at the time. During these first 8 test days, the only available host is an *A. smithi* larva within which is the first hyperparasitoid, *A. megourae* (Table 1). The second hyperparasitoid, *D. carpenteri,* continues to feed externally, and there is no possibility of direct tertiary parasitoidism on an *A. megourae* larva, although this first hyperparasitoid is indirectly consumed because at this time, it is still within the *A. smithi* larva.

### Test days 1–8

Based on 152 adults that emerged from mummies of these first 8 test days, the average of the two hyperparasitoids was 50.7% *A. megourae* and 49.3% *D. carpenteri.*

### Test days 9–10

Beginning with test day 9, as explained above, an *A. megourae* larva emerges from an *A. smithi* host inside the mummy and is exposed for the first time to direct attack by a *D. carpenteri* female (Table 1). Only now could true or direct tertiary parasitoidism occur, and it might be expected that at least beginning with these 2 days, the second hyperparasitoid, *D. carpenteri,* would be more successful. Yet, of the 40 adults that emerged from mummies of test days 9 and 10, the averages were equal: 50.0% *A. megourae* and 50.0% *D. carpenteri.*

### Test days 11–17

The remaining test days 11–17 are grouped together because they represent a marked drop in the success of *D. carpenteri.* Of the 149 hyperparasitoids that emerged, only 8.1% were *D. carpenteri.* This failure at tertiary parasitoidism resulted in 91.9% of the emerged adults being *A. megourae.* In fact, no *D. carpenteri* emerged on the last 3 test days (15–17).

### Evaluation

Although there is definitely some tertiary parasitoidism by *D. carpenteri* during test days 9–14 (when *A. megourae* becomes available for attack), the success rate is quite low. This is especially evident as the diminishing emergence of this second hyperparasitoid drops to zero during the last 3 test days when no *D. carpenteri* emerged, thus lowering the average for test days 11–17 to 8.1%. This was not entirely unexpected, however, because it had already been reported,[20] that in the latter days of development in similar experiments using 2 different hyperparasitoid species, *Alloxysta victrix* pupae and preadults become highly sclerotized. This deterred oviposition and tertiary parasitoidism by the second hyperparasitoid, *Asaphes californicus.* This also occurs between *A. megourae* and *D. carpenteri.*

Low success at tertiary parasitoidism was also reported intraspecifically between *Dendrocerus carpenteri* attacking another *D. carpenteri,* wherein the second hyperparasitoid had a success rate of only 8.0%.[1] It was suggested that a defensive behavior (violent twitching) and morphological changes (spine-like projections and a posterior conical process) in fourth instar larvae of *D. carpenteri* caused this relative failure at tertiary parasitoidism by the second *D. carpenteri.* Also, the venom of *D.*

*carpenteri* may have been less effective against its own species (intraspecific immunity) than against the more susceptible *Aphidius smithi* primary larva as shown in the color plate published by Bocchino and Sullivan in 1981.[2]

## Host Specificity

Another explanation for this low success rate at tertiary parasitoidism by *D. carpenteri* may be a certain degree of "host specificity" that we did not suspect. Normally, we have no problem in rearing *D. carpenteri* on *A. smithi* in the laboratory when maintaining the colony. It is even the dominant hyperparasitoid (64.7%) in New Jersey alfalfa fields when *Aphidius ervi* Haliday mummies were collected over a 3-yr period and the hyperparasitoids permitted to emerge in the laboratory.

For many years, host specificity had been discounted among the hyperparasitoids, but evidence to the contrary has gradually been presented that this may not be true for the genus *Alloxysta*.[3, 5, 7, 21, 23] Perhaps *D. carpenteri* is another example of a hyperparasitoid displaying some degree of host specificity. It may be that a host other than a primary parasitoid larva such as *Aphidius* spp. is unsuitable either for oviposition or larval development. It should be remembered that feeding behavior with regard to number of species eaten is a continuum, and that it is only for convenience that at each end of this spectrum, the terms monophagy and polyphagy are used. With this in mind, van den Bosch had emphasized that "host specificity" should not have a restricted meaning, but can range from monophagy to some level of oligophagy.[23] He predicted that further study of hyperparasitoids would reveal a kind of flexible host specificity in other groups similar to that shown in the genus *Alloxysta* that is an endoparasitoid. Perhaps *Dendrocerus carpenteri,* as demonstrated in this present research, is one more example. This would be especially interesting because *D. carpenteri* is an ectoparasitoid, and therefore in a class usually considered more polyphagous.

## Mortality

Of the 420 mummies used in these experiments, 79 or 18.8% showed no parasitoid emergence, neither *A. smithi, A. megourae* nor *D. carpenteri.* These mortality results are similar to the three other parallel experiments on tertiary parasitoidism conducted under similar laboratory conditions referred to earlier: *Alloxysta victrix* and *Asaphes californicus* (18.0%),[20] *Dendrocerus carpenteri* and *D. carpenteri* (15.0%),[1] *Asaphes lucens* and *A. lucens* (20.0%).[13]

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